THE TIME BUDGET AND FEEDING ECOLOGY OF THE PUKEKO

Porphyrio porphyrio melanotus

Temminck, 1820

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John D. Wright

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ABSTRACT

The annual and seasonal time budget and feeding ecology of pukeko Porphyrio porphyrio melanotus are described both as a composite day and diurnally. The study shows pukeko do not spend equal time in all activities in all habitats over the day, for each season or over the year. They spend by far the bulk of their time feeding (75-90%), and less time to attentiveness, bodily maintenance, and social encounters. However time allocated to all activities varies with habitat. By far most time is spent in dryland (pasture), and less in turn in rush margins, swamp and water. Bimodal activity patterns (dawn and dusk) are described for each season, whereas feeding effort is unimodal peaking in the mid to late afternoon. Direct sampling of an adjacent population indicates pukeko gradually increase the length of tiller taken and quantity of ingesta consumed over the day. Pukeko do not peck at the same rate or feed at the same intensity in all habitats, at all times of the day, for each season or over the year - feeding fastest and most intensely in rush margin and mud areas, and slower and less intensely in dryland, swamp and water. However considering use of habitats over the year pukeko feed most intensively and extensively in dryland, but less in rush margin, mud, swamp and water. Feeding in the latter three habitats is linked notably with seasonal availability (and/or quality) of forage. Evidence indicates pukeko are able to gauge seasonally the availability (and/or quality) of forage, and allocate their feeding effort appropriately.

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1. INTRODUCTION

The pukeko Porphyrio porphyrio melanotus (Temminck), is a non-endemic native, swamp or wet-land dwelling gallinule, found commonly throughout New Zealand. It belongs to the widely distributed genus Porphyrio which, according to Vielliard (1974) "ranges over the Old World in four basic types of colouration. The nominate form, entirely violet, is endemic to the western Mediterranean region; and the madagascariensis group of tropical Africa, Madagascar and Egypt has a green back contrasting with blue remiges and underbody. The poliocephalus group, from Turkey to Indo-China, is light blue with the head pale grey; this passes, in Malaysia, into the melanotus group of very pigmented forms, the head and back becoming almost black, across the Australasian region" - further the same sub-species is found in the south and east of Australia, New Guinea, New Caledonia, Norfolk Island, Lord Howe Island, and Tasmania (RAOU., 1926).

From evidence of sub-specific characters, between New Zealand's pukeko and Australia's Eastern Swamphen, Fleming (1962) regards the pukeko as a late arrival in New Zealand, around the late to middle Holocene period, i.e. 10-15,000 years ago, "showing, in European times, all the vigorous adaptability of a new immigrant, remarkably versatile in a rapidly-changing environment" (Falla, 1953).

Detailed knowledge of the seasonal, let alone diurnal, food habits of pukeko, as with all rails, is scarce, although Buller (1877) described the pukeko as "semi nocturnal in its habits, being most active after dusk." Muggeridge and Cottier (1931), working in conjunction with the Wildlife Service, Internal Affairs, Wellington, and local Acclimatisation Societies, investigated their food habits, by studying the gizzard contents of 63 birds. They were taken from Auckland, Wellington, North Canterbury, Southland and Otago, being ideally collected at a rate of two birds from the vicinity of crops, and from swamp land distant from crops,

i.e. in all 20 birds each month. However, local branches of the Acclimatisation Societies were unable to supply the appropriate number of birds. The time of day at which the birds were shot, as well as the habitat over which they were shot, were unrecorded. At that time, and to the present, Acclimatisation Societies and farmers appeared to be at a difference of opinion, concerning the effects of pukeko on crops and pasture. The farmers believed the birds were the source of great damage to crops and pasture, (see also Bell, 1955), and spread disease (e.g. Salmonella), while the Acclimatisation Societies, believing that pukeko were mainly insectivorous, contended that the good accruing from the number of injurious insects destroyed, outweighed any damage that might be done to the crops. Muggeridge and Cottier, however, concluded that pukeko were primarily vegetarian, and that insects did not form a staple part of their diet, even given that insect remains were rendered unidentifiable more readily, and did not persist as long as, the vegetative portion of the diet.

Tunnicliffe (1965), following preliminary accounts by McLean (1902) and Guthrie-Smith (1927), studied the pukeko's general biology, presenting details of distribution, the laying season, breeding cycle, moult, measurements and weights of captured birds, and also behaviour. He did not study the feeding patterns of pukeko.

Carroll (1966), in an attempt to define the pukeko's food habits, to dispel old arguments that once again had arisen between farmers and Acclimatisation Societies, arranged for the collection of 298 pukeko gizzards, from throughout New Zealand, and at all times of the day. From analysis of gizzard contents, she attempted to determine the foraging habitat over which the birds were shot, and also to measure the relative importance of marginal habitats to the overall feeding effort of the birds. Shooters were asked to note the time of shooting (as either early morning, mid-day, or late afternoon), and to define the habitat over which the birds were shot (as either swamp, pasture, or a swamp/pasture mixture), and for these reasons definition

of habitat was largely subjective.

Her results confirmed Muggeridge and Cottier's, in that most gizzards contained plant remains and only a few had insects. Significantly also, a number of gizzards contained oats, barley and other cereals. The most abundant material, found in 70% of the gizzards, was the grasses, especially Poa spp. and less importantly Glyceria spp., Holcus and Anthoxanthum. "There appeared to be no preferential selection of grass seeds as items of food; instead, they were always associated with other parts of the plant. Most favoured portions were the tender stalk-bases, although often the whole plant was eaten, being snipped by the sharp beak of the pukeko into approximately quarter-inch sections, as if by a pair of scissors. Vegetative parts of sedges appeared in 56% of gizzards, not only were stalks, leaves, and rootstocks eaten, but the fleshy tubers, whole or fragmented, were often found to form the bulk of the meal. Sedge seeds frequently occurred in considerable quantities." Other species eaten included Eleocharis, Scirpus, Carex, Cladium, and Mariscus. Seeds of rushes, Juncus spp., occurred in 15% of all stomachs. Dicotyledonous leafy material found in gizzards was almost exclusively clover, occurring in 34% of the specimens. Other plants eaten included Polygonum spp. and Rumex spp., as well as Bidens, Stellaria, Ranunculus, Salvinia, Lemna, Zannichellia, Potamogeton, and Elodea - the latter group being consumed infrequently.

Over the day, gradually less plant food (dry weight) was found in the digestive tract, but because the birds were not sampled consistently throughout the year the results are probably distorted.

Data on the utilisation of each habitat was inconsistent, as the bird's gizzards seldom held pasture or swamp plants exclusively. However Carroll concluded "pukeko forage at all times of the day, although perhaps less in the afternoon and evening ... and ... it appears the birds feed as they move about in a particular habitat, which normally includes swamp, damp pasture, and grassland. Seeds, predominantly those of sedges, rush, grass, sorrel, and dock are eaten in

season. Grasses, clover leaves and the more tender portions of swamp plants form their staple diet throughout the year."

McKenzie (1967), pointing out that raupo Typha and other "fringe" foods, such as blackberry Rubus spp., had not shown up in Carroll's analysis of stomach contents, quoted experiences of seeing pukeko taking carrion (see also - McLean, 1902; Oliver, 1930 and 1955; Bryant, 1940; Gorgas, 1968; Craig, 1974, and personal observation), and eggs (see also - Oliver, 1930 and 1955; Bryant, 1940; Fitzgerald, 1966; Fogarty, 1968; Gorgas, 1968; Barlow et al., 1972 and Craig, 1974) of waterfowl. He suggested a possible modification of the pukeko's diet since the times of Buller (1877) and Oliver (1930), which was probably paralleled by habitat modification, such as drainage of swamps, and establishment of highly productive pastures.

From 1971-1973, Fordham (unpub.) periodically observed pukeko occupying two areas, pasture and swamp, for two to three hours prior to sunset at Pukepuke Lagoon, Himatangi - a Game Management Reserve, under the control of the Wildlife Branch, Department of Internal Affairs. Data combined from all years, indicated the birds in pasture spent most time feeding in winter (83.3%; n=875 bird-observations), followed in turn by autumn (82.6%; n=2773 bird-observations), spring (69.3%; n=647 bird-observations) and summer (79.9%; n=1220 bird-observations), while in swamp they were seen feeding most frequently in winter (67.2%; n=1055 bird-observations), and least often in spring (55.1%; n=321 bird-observations). Throughout the year the birds spent more time feeding in pasture than in swamp. Rates of feeding in these and other marginal areas of the lagoon were not measured.

Caithness (1973), referring to Fordham's (unpub.) work, commented that "examination of faeces and direct observations show that pukeko mostly feed in the belt of pasture closest to the lake. Here pasture growth in enclosures, which deny entry to the birds, suggest that pukeko have a considerable influence."

Recently Craig (1974) investigated the year-round social organisation of the pukeko in two areas of differing habitat. Subsequent publications include Craig 1976 and 1977.

Special emphasis was given to assessing the interaction of social hierarchy and territory, and the role of communal breeding. He observed that "pukeko were mainly herbivorous, although quantities of animal food were taken in the breeding season, and fed mainly to chicks." He found pasture provided most of the food outside the breeding season, but when nesting or caring for young chicks, pukeko confined their activities to the swamp, where they fed mainly on raupo.

Within New Zealand, the takahe Notornis mantelli is the pukeko's closest relative, sharing rather unusually, a similar ecto-parasitic mite spp. (Holloway, 1955; Pearce, 1976). Since its re-discovery in 1948 in the Murchison Mountain Range, Fiordland National Park, much time and effort has been devoted to gathering information on this bird's feeding habits, in an attempt to understand, and perhaps prevent further reduction of the remaining population.

Generally feeding activities pursued by this bird (Falla, 1949; Smith, 1952; Gorgas, 1968), are similar to those described for pukeko (see later). Gurr (1951) found that most remains in takahe chick faeces, were of insects whereas Falla (1949), Williams (1952, 1960), Secker (1953), Reid (1967), Gorgas (1968) and others, have found the adults are almost entirely vegetarian, - the rearing success of takahe chicks being related to the quality of food within a territory (Kean, 1956). Moreover, the quality of the bird's diet in relation to its daily energy requirements has been investigated (Reid, 1974).

Research was then directed towards determining the population dynamics of takahe, particularly the difference in mortality and recruitment rates that existed between habitats of varying quality of preferred food plant spp., (Mills and Lavers, 1974; Mills, 1975), and the possible effects of competition from red deer Cervus elaphus (Mills, 1976).

Most recently however, seasonal analysis of macronutrients of preferred sub-alpine food spp., and observations on the food preferences and feeding rate of takahe (Williams et al, 1976b; Mills and Mark, 1977), have shown the presence of a

food preference rank for snow tussock Chionochloa spp., which corresponded to the relative amounts of major nutrients (especially phosphorus) and sugars they contained. Selection between plants of the same species for the highest levels of phosphorus occurred in spring, early summer and autumn, while in winter, the birds switched from snow-covered sub-alpine plants to feed primarily on the summer-green fern Hypolepis millefolium found in the sub-alpine Mountain Beech Nothofagus solandri var. Cliffortioides forests.

Work on other closely related rails, e.g. Purple Gallinule Porphyrula martinica, indicates omnivory in adults (Meanley, 1963), while the chicks are primarily insectivorous (Trautman and Glines, 1964).

Carroll (1963) studied the food habits of 94 North Island Wekas, Gallirallus australis greyi, taken from Waimata Valley, East Coast district, North Island. Oliver (1955) wrote that the birds consumed large quantities of grass-grubs, and other noxious insects, rats and mice, as well as an assortment of vegetable material. Although primarily carnivorous, wekas were found to be omnivorous, eating especially grass leaves and stalks, fibrous material, small pieces of wood, clover leaves, and less frequently small leaves (e.g. manuka Leptospernum scopathium) and moss - a total percentage volume, excluding seeds, of 55.68 cm^3, and percentage dry-weight of 46.17 gms. Monthly data indicated most vegetable matter was eaten in winter, while most animal matter and seeds were taken in spring and summer. Insects predominated in the animal food taken - the most important being beetles, wetas, and grass hoppers. Earthworms were also a major item of the diet, while insect eggs and millipedes were frequently found.

From preliminary work, the endangered Lord Howe Island Woodhen Gallirallus sylvestris appears to feed on almost any invertebrates found during foraging on the forest floor and in lower parts of the vegetation, and not to eat fruit from forest trees. They have also been observed eating eggs

and chicks of the Providence Petrel Pterodroma solandri, but the latter may be carrion-feeding and not predation (Fullagar and Disney, 1975).

Recent studies of Tasmanian native hen Tribonyx mortierii show adults, consuming mainly the short, young shoots of grass and low herbs, and seeds (Ridpath, 1964, 1972a), act as secondary grazers, and are dependent on other animals e.g. sheep and rabbits, for the primary mowing effect (Ridpath and Moreau, 1966; Ridpath, 1972b), while the young are insectivorous (Ridpath, 1972a). Concerning the effects of these birds on oat crops, Ridpath and Meldrum (1968) noted a reduction of weight of the yield at six-eight weeks after sowing, of 24-36% on the immediate edge of one margin of a paddock that bordered water. For the entire paddock the reduction in weight attributable to native hen feeding activities, was 8% - an estimate similar to that given to damage on the same crop caused by rabbits. Ridpath, (1972a) observed that native hens grazed steadily all day, within their territories, pecking at a rate of c. 100 pecks per minute which was considerably faster than that recorded for pukeko (c. 38 pecks/min.). However, no detailed seasonal or diurnal activity pattern, or feeding rate studies were carried out.

Fordham (1978) noted that while detailed descriptive work had been carried out on moorhen Gallinula chloropus behaviour, breeding biology, and sexual discrimination (references therein), feeding ecology had not attracted much attention. Feeding intensities of moorhen at dawn and dusk in late winter and spring were indexed by scoring activity frequencies, and combining the frequency of feeding with the rates at which birds pecked. Results indicated that both the frequency of feeding and pecking rates were higher before sunset, than after sunrise. The feeding intensity and time allocated to feeding during the central daily periods were not investigated.

Hence, knowledge of the seasonal and diurnal variation of time allocated to various activities for rails as a whole,

and pukeko in particular, is scarce. This study was intended to fill, at least a few of these gaps. The aims of my project were:

1. To determine for each season the diurnal changes in time allocated by pukeko to various activities, e.g. feeding, alertness, con-specific agonistic encounters, bodily maintenance, courting, and other activities.
2. To determine, seasonally and diurnally, the feeding intensity (following Fordham, 1978, - calculated from time spent eating and pecking rates) for an "average" bird of the flock feeding in any one of the five habitats recognised in the study area (i.e. dryland, rush margin, mud region, swamp and water).
3. To determine diurnally and seasonally, the relative importance of each habitat to an "average" feeding pukeko at Hamilton's Lagoon.
4. To determine, by direct sampling, diurnal food intake patterns of pukeko, as a check on the indirect measures of feeding intensity.